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A silviculture-oriented spatio-temporal model for germination in *Pinus pinea* L. in the Spanish Northern Plateau based on a direct seeding experiment

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Abstract Natural regeneration in *Pinus pinea* stands commonly fails throughout the Spanish Northern Plateau under current intensive regeneration treatments. As a result, extensive direct seeding is commonly conducted to guarantee regeneration occurrence. In a period of rationalization of the resources devoted to forest management, this kind of techniques may become unaffordable. Given that the climatic and stand factors driving germination remain unknown, tools are required to understand the process and temper the use of direct seeding. In this study, the spatio-temporal pattern of germination of *P. pinea* was modelled with those purposes. The resulting findings will allow us to (1) determine the main ecological variables involved in germination in the species and (2) infer adequate silvicultural alternatives. The modelling approach focuses on covariates which are readily available to forest managers. A two-step nonlinear mixed model was fitted to predict germination occurrence and abundance in *P. pinea* under varying climatic, environmental and stand conditions, based on a germination data set covering a 5-year period. The results obtained reveal that the process is primarily driven by climate variables. Favourable conditions for germination commonly occur in fall although the optimum window is often narrow and may not occur at all

in some years. At spatial level, it would appear that germination is facilitated by high stand densities, suggesting that current felling intensity should be reduced. In accordance with other studies on *P. pinea* dispersal, it seems that denser stands during the regeneration period will reduce the present dependence on direct seeding.

Keywords Empirical modelling · Two-step regression · Regeneration · Stone pine

Introduction

Pinus pinea is an essential species in Mediterranean ecosystems, its timber and edible seed production generating important economic benefits to the local population. In addition, the species plays a valuable ecological role since it frequently occupies sites with challenging climatic and edaphic conditions (Mediterranean climate and highly sandy soils) where few arboreal species persist. Such conditions are common throughout the Spanish Northern Plateau (Prada et al. 1997), where there are more than 50,000 ha of managed *P. pinea* forests.

Natural regeneration of this species has become a primary concern for forest management. Like other large-seeded Mediterranean species, natural regeneration is commonly unsuccessful under the silvicultural regimes and regeneration methods currently applied (high-intensity thinnings, seed-tree and increasingly, the shelterwood method), which lead to low stand densities. Several factors underlying this regeneration failure have been identified including climate (specifically, severe summer droughts and high summer temperatures that result in establishment failure); masting habit and lack of synchrony with regeneration fellings on the one hand and suitable years for

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seedling establishment on the other; intensive cone harvesting, resulting in depauperate seed banks prior to regeneration felling; long rotations, inducing poor seed crops during the regeneration period due to a decline in tree vigour; the gravity-based seed dispersal strategy of this species, resulting in patchy seed distribution; and post-dispersal seed predation (Barbeito et al. 2008; Calama and Montero 2007; Manso et al. 2010; Manso et al. 2012). As a result of these difficulties, massive direct seeding has been commonly applied in the Northern Plateau in order to ensure regeneration of *P. pinea* stands (Gordo et al. 2012). However, little is known about germination performance under field conditions when direct seeding takes place. Although the technique has proved effective so far, there exists a gap of knowledge concerning the factors that maximizes emergence and, in turn, that would minimize the seeding effort. On the one hand, climatic variables are essential to understand average germination rates across the region. On the other hand, silvicultural factors are controllable and studying their effects can provide managers with new insights to regenerate the stands. In this respect, it is of particular interest to investigate whether the higher stand densities suggested to reduce seed limitation (Manso et al. 2012)—and therefore, the necessity for seeding—will promote or hamper seed germination.

Typically in forestry, germination studies have been conducted under controlled conditions to ‘untangle’ species dormancy trends (Skordilis and Thanos 1995; Nomiya 2010; Cook et al. 2008; Cooke et al. 2002), to shed light on optimum temperature and humidity conditions (Lippai et al. 1996; Cochard and Jackes 2005; Magini 1955), to investigate the influence of light on the process (Silveira et al. 2004; Honda and Katoh 2007; Seiwa et al. 2009), to determine germination facilitation after fire (Baeza and Roy 2008; De Luis et al. 2008; Ooi 2010) or to explore germination responses to topsoil conditions (Puerta-Piñero et al. 2006). Among the few studies carried out either partially or completely through field trials, only general climate comparisons (Ordóñez et al. 2004; Meyer and Pendleton 2005), particular climatic events (Ruano et al. 2009) and understory composition (Keyes et al. 2009) have been evaluated in relation to germination.

Although these studies provide fundamental data on seed ecology, they commonly lack essential information for determining the successful occurrence of germination under the full range of conditions potentially affecting the process, which could be particularly important in the case of *P. pinea*. Calama et al. (2012) reported that germination in the Northern Plateau stands occurs only under very restricted climatic conditions, which do not necessarily arise every year. Hence, further research should be undertaken to accurately predict the degree of success in germination in response to continuous climatic variables

under different silvicultural systems. Also, providing that soil preparation is conducted before proceeding with direct seeding, germination performance has to be tested directly on the mineral soil. Suitable predictive models have been proposed in agronomy and seed science literature such as the hydrothermal model (Bradford 1990; Roman et al. 2000), based on the cumulative effect of water potential and temperature on the cumulative germination rate. Hardegree et al. (2003) proposed a simulation through intensive laboratory experiments to predict field germination rates. However, as these interesting studies were not developed within a forestry management framework, they do not include stand-related variables, inherently useful to foresters, but commonly utilize explanatory variables which are not easily collected by forest managers or which are difficult to relate to silvicultural practices (i.e. water potential).

Therefore, we propose a different modelling approach that takes into account management necessities. To achieve this objective, a long term direct seeding field experiment was installed in the Northern Plateau to record germination behaviour under a highly diverse set of climatic, environmental and management conditions.

The main aim of this study was to model the germination response of *P. pinea* to varying environmental, climatic and stand conditions when direct seeding is carried out. The model will allow us to identify the factors regulating germination and to draw conclusions as regards the measures to be taken by forest managers in order to encourage this essential process and reduce direct seeding. Specifically, we hypothesized that the implementation of more progressive felling schedules may have a positive effect by modifying determinant factors for germination. In this respect, our findings will provide a valuable resource for management decision-making in *P. pinea* forests where direct seeding is conducted to make successful regeneration possible.

Materials and methods

Study site

The study site is located at 700 m a.s.l. in a representative *P. pinea* stand on the flat sandy soils of the Northern Plateau, Spain. The study was conducted in a 120-year-old even-aged pure stand in *Corbejón y Quemados* public forest (41°28'N, 4°43'W). The site location was selected and regeneration felling treatments designed to represent typical conditions in a mature managed forest, ranging from the shelterwood system to seed-tree method. Regeneration fellings commenced in 2002–2003. Pre-felling and post-felling stand densities are shown in Table 1. The

climate is continental-Mediterranean with mean monthly temperatures ranging from 4.0 °C in January to 21.7 °C in July. Mean annual precipitation is 435 mm, with a period of summer drought (July to September, mean precipitation of 66 mm). The site index is 15–16 m at 100 years; characteristic of a class II quality (Calama et al. 2003).

Within the same study site, different experiments related to the overall process of natural regeneration in *P. pinea* (seed dispersal, predation, physiological status, establishment and survival) in the Northern Plateau have been carried out (Madrigal et al. 2011).

Experimental design

The germination trial was installed in July 2006. It consisted of two 60 m × 80 m (0.48 ha) sample plots that were set up under two different regeneration management stand densities. A 7.5-m buffer area was included around each plot, increasing the overall plot area to 0.7 ha. All trees within plots were stem mapped and their relative coordinates within each plot calculated. Eighteen seed points were deployed throughout each plot. Seed point location was chosen so as to include a wide natural light gradient and two cover conditions (litter and grass). The relative coordinates of each point were also recorded. Seed points were protected with a 40 cm × 40 cm × 15 cm cage made of hard wire mesh (span 0.7 cm × 0.7 cm), fixed to the ground with nails to minimize rodent predation. The cages could be opened from the top to permit seed manipulation and were buried 3 cm deep to allow direct seed-soil contact.

On 1 August 2006, 2007, 2008, 2009 and 2010, 50 seeds were placed on the ground in each cage. This date was chosen because natural seed release, which commences in the beginning of the summer season, can be assumed to be mostly completed at that point (Manoso et al. 2012). In addition, direct seeding is usually conducted by early fall (September). The seeds were provided by the Forest Service of the Regional Government of Castilla y León. Seed collection systematically takes place in Tordesillas Selected Stand, nearby the study area, from an average population of 5,136 individual trees (Gordo 2002). The seed lots had been previously tested using the ISTA protocol (viability 91.55 %). No stratification or imbibition treatment was applied.

Each year, germinated seeds were counted and discarded at regular fortnightly intervals (averaging 17.56 ± 1.06 days) up to the following August or until complete germination was reached. Henceforth, the term year will be used to refer to these annual measurement intervals. Sample plots were visited on a total of 80 occasions. The criterion used to consider seeds as germinated was the presence of a radicle protruding at least 0.2 cm beyond the seed coat. During the periods 2007–2008 and 2008–2009, a plague of *Apodemus sylvaticus* in Northern Spain caused some damage at several seed points, which were discarded from analysis.

Daily climate variables were obtained from Olmedo meteorological station, located 15 km from the study site and at the same altitude (41°17'N, 4°40'W; data available in www.inforiego.org). To estimate light availability at each seed point, Global Site Factor (GSF) was calculated from hemispheric photographs taken at each cage location. The water-holding capacity (WHC) of the uppermost layer of the soil was obtained for each point through texture analysis of two soil samples taken in the close vicinity of the seed points. The uppermost 20 cm of the soil profile were extracted for each sample (1.57 dm³ soil cylinder). Finally, in order to consider the possible influence of trees on microclimate conditions at ground level, the influence potential (IPOT) of all trees located within a 15-m radius was calculated for each seed point. IPOT is a competition index based on the concept of ecological field theory (Wu et al. 1985), empirically modified by Kuuluvainen and Pukkala (1989):

$$IPOT_j = 1 - GPOT_j$$

where

$$GPOT_j = \prod_{h=1}^{n_j} (1 - I_{hj}) \text{ and } I_{hj} = (dbh_{hj} / \max(dbh_h)) \times \exp(-b \cdot d_{hj}) \quad (1)$$

I_{hj} is the potential influence of tree h at seed point j , d_{hj} is the distance from tree h to seed point j , dbh_{hj} is the diameter at breast height of tree h in the seed point j influence area, $\max(dbh_h)$ is the maximum dbh_h at each plot, b is a parameter, and n_j is the number of trees in the seed point j influence area. Heuristically, we set a value of 0.25 for b . IPOT ranges from 0 (no competition) to 1 (maximum competition).

Table 1 Summary of stand densities

| Plot | N b/f (ha ⁻¹) | BA b/f (m ² /ha ⁻¹) | Dg b/f (cm) | N a/f (ha ⁻¹) | BA a/f (m ² /ha ⁻¹) | Dg a/f (cm) | H a/f (m) | FCC a/f (%) |
|------|---------------------------|--|-------------|---------------------------|--|-------------|-----------|-------------|
| 1 | 156 | 18.80 | 39.2 | 46 | 6.99 | 44.1 | 12.6 | 14 |
| 2 | 192 | 22.29 | 38.4 | 73 | 10.82 | 43.4 | 14.1 | 31 |

b/f–a/f before fellings–after fellings. N is the stand density; BA is the basal area; Dg is the quadratic mean diameter; H is the average height; FCC is the forest canopy cover

The range and distribution of the spatial variables is shown in Fig. 1.

Data analysis

Interannual and seasonal pattern of germination

Two preliminary analyses were undertaken to identify general traits of variability in germination response. Firstly, the seasonal germination pattern was studied using exploratory analysis. The following germination traits were compared between experiment years: starting date of the germination process, proportion of germinated seeds within seasons and maximum germination proportion within a measurement interval. Secondly, the annual proportion of germinated seeds was compared through a binomial generalized linear model with a logit link function, considering each seed point as a sample unit and year as factor.

Modelling germination

In order to model germination with respect to climatic (temporal) and environmental (spatial) covariates, the response variable used was the number of seeds germinated in a specific period i and seed point (n_{ij}) with respect to the total amount of non-germinated seeds at the beginning of period i , divided by the duration of the period (d_i), in days:

$$pg_{ij} = \frac{n_{ij}}{(N_j - \sum_{i=1}^I n_{i-1,j}) \cdot d_i} \quad (2)$$

where N_j is the initial number of seeds in seed point j , and I is the total number of intervals.

Thus, pg_{ij} will give the seasonal decrease in the seed bank over time. However, three main statistical limitations arose when modelling this variable: (a) germination often exhibits an intermittent pattern, which leads to a zero-inflated frequency data distribution (violating standard normality assumptions); (b) lack of independence among observations within sample units and measurement years,

possibly exhibiting non-trivial dependencies among the within-group errors; and (c) the nature of this variable could inherently imply heteroscedasticity of residuals over time-varying covariates. To deal with the first issue, the likelihood of germination dependence on different covariates was studied considering two different processes separately: germination occurrence and germination abundance. Through the analysis of previous graphical residual patterns, the problems derived from independence and homoscedasticity violation were corrected by including random effects, allowing for auto-correlation error structures in the variance–covariance matrix and applying weighted variance in model formulation.

Germination occurrence Modelling germination occurrence was performed using a binary variable that equals 1 when a seed point has germinated seeds during a period i (thus, $pg_{ij} > 0$) and zero if not. A logistic regression was computed via logit link function to model the process. We considered temporal and spatial variables in model formulation. Several temporal variables were tested, namely; the proportion of days with precipitation occurrence (Pp_i), proportion of freezing days (Fr_i), averaged daily values for the mean relative humidity of the air (Hr_i ; ratio of the partial pressure of water vapour in the air to the saturated vapour pressure of water) and alternately, mean, maximum and minimum temperature (T_i), for each collection period (i.e. fortnight prior to measurement). The spatial variables were GSF_j , $IPOT_j$ and WHC_j (continuous); and cover conditions C_j (categorical factor with two levels, litter = 0 and grass = 1), evaluated at each seed point j .

Model parameterization was carried out as follows: the logit-transformed probability of germinated seed presence at a seed point j during a period i (p_{ij}) is assumed to be linearly related to Hr_i , Pp_i , Fr_i , GSF_j , $IPOT_j$, WHC_j , C_j , and to a function of T_i ($f_1(T_i)$). There is an optimum temperature at which the germination response is maximized (Bewley and Black 1994), so that the suitable thermal range can be described by the cardinal temperatures of species [base (T_b), optimum (T_o) and maximum (T_m);

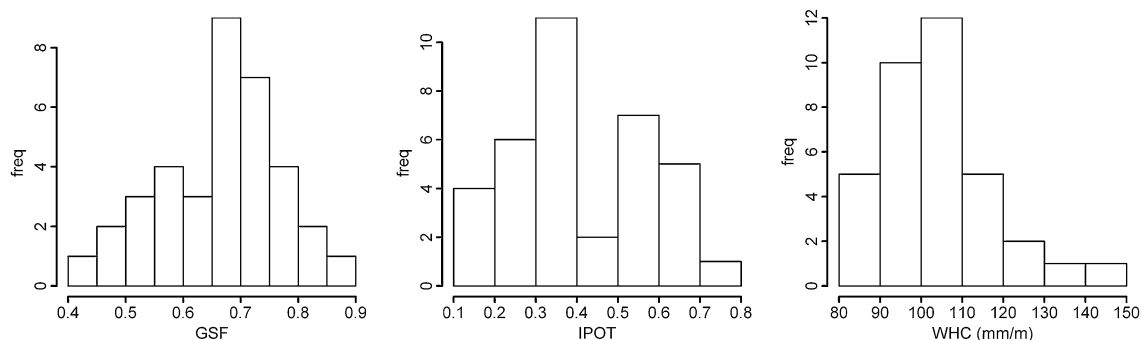


Fig. 1 Histograms of the considered explanatory spatial variables. GSF is the Global Site Factor; IPOT is the influence potential; and WHD is the water-holding capacity

Kamkar et al. (2012)]. Therefore, $f_1(T_i)$ was defined to fulfil these conditions. We tested two different hypotheses for $f_1(T_i)$ based on the skewness of the germination response (Eqs. 3 and 4):

$$\text{if } T_o - T_b = T_m - T_o \quad f_1(T_i) = \alpha_1 + \beta_1(T_i - \mu_1)^2 \quad (\text{no skewness}) \quad (3)$$

$$\text{else} \quad \begin{cases} f_1(T_i) = \alpha_2 + \beta_2 T_i & \text{if } T_i \leq T_o \\ f_1(T_i) = \alpha_3 + \beta_3 T_i & \text{if } T_i > T_o \end{cases} \quad (\text{skewness}) \quad (4)$$

Parameter μ_1 holds an ecological meaning, representing the value of T_i that maximizes germination occurrence (T_o) whereas the linear relation is controlled by parameters $\alpha_1 \neq \alpha_2 \neq \alpha_3$ and $\beta_1 \neq \beta_2 \neq \beta_3$ as intercepts and slopes, respectively. Note that under the skewness hypothesis, $T_o = (\alpha_2 - \alpha_3)/(\beta_3 - \beta_2)$. The complete model is shown in Eq. 5:

$$\log\left(\frac{p_{ij}}{1 - p_{ij}}\right) = f_1(T_i) + \theta \text{Hr}_i + \lambda_1 \text{Pp}_i + \tau_1 \text{Fr}_i + \gamma_1 \text{GSF}_j + \kappa_1 \text{IPOT}_j + \eta_1 \text{WHC}_j + \rho_1 C_j \quad (5)$$

As measurements are repeated over time in the same plots and seed points, correlation can be present given the data structure. Field visits are grouped into different years, which implies a crossed random effect with respect to both plot and seed point level variability. In order to correct data correlation, we attempted to include random terms in the model fit. We expanded the model intercept (s) to allow for random effects at seed point (u_{jk}), plot (v_k ; i.e. regeneration treatment) and year (w_l) level. Interactions between random effects and between random and fixed effects were not considered.

The model selection was carried out by comparing the Akaike Information Criteria (AIC) values produced by the different fits, providing all fixed effects and random variance components were significant.

Once the best model had been selected, we heuristically estimated the value of a cut-off that optimized specificity (rate of correctly classified non-events) and sensitivity (rate of correctly classified events).

Germination abundance Germination abundance modelling was conducted conditioned to germination occurrence (i.e. using only non-zero values). Therefore, pg_{ij} was modelled through a nonlinear mixed model (the response variable was previously logit-transformed to achieve normality; note that this is not strictly a logistic regression as we do use the normal likelihood function). Based on previous graphical analysis, the regression model was parameterized considering logit (pg_{ij}) as a linear function of relative humidity with intercept parameter α_4 and a slope term. The latter was expanded as a function of

mean, maximum and minimum daily temperature $f_2(T_i)$, alternately. This function was defined as $f_1(T_i)$ in the occurrence model, as germination capacity and germination rate are similarly influenced by temperature (Bewley and Black 1994). In order to test the skewness of the response, we substituted Eq. 3 with a normal density function for the symmetry hypothesis. The normal density is defined by parameters μ_2 and σ^2 , where μ_2 represents the value of the temperature at which the germination rate is maximized. As regards the skewness hypothesis, Eq. 4 was used. With respect to other covariates, the same ones were tested as in the occurrence model since there was no prior evidence of different factors driving each process. Thus, linear terms depending on Pp_i , Fr_i , GSF_j , IPOT_j , WHC_j and cover type C_j were inserted in the model, along with corresponding slope parameters λ_2 , τ_2 , γ_2 , κ_2 , η_2 and ρ_2 . Further interactions were not taken into account for model simplicity. Possible spatial and among-year patterns of unobserved dependence were modelled including random effects. Different levels of variability were attempted on model intercept [seed point (u_{jk}), plot (v_k ; i.e. regeneration treatment) and year (w_l)], avoiding interaction terms among random effects or random and fixed effects. Once the optimal variance structure was set in the saturated model, covariate selection was carried out by fitting models with different fixed effects alternatives and comparing their AIC values (Zuur et al. 2009). In Eq. 6, the model without random effects, including the intercept α_4 and the residual term ε_{ij} , is shown.

$$\log\left(\frac{\text{pg}_{ij}}{1 - \text{pg}_{ij}}\right) = \alpha_4 + \lambda_2 \text{Pp}_i + \tau_2 \text{Fr}_i + \gamma_2 \text{GSF}_j + \kappa_2 \text{IPOT}_j + \eta_2 \text{WHC}_j + \rho_2 C_j + f_2(T_i) \times \text{Hr}_i + \varepsilon_{ij} \quad (6)$$

Goodness of fit and model evaluation Assessment of goodness of fit in the occurrence and abundance models was performed through graphical analysis of residuals. Any detected pattern would suggest altering the variance estimate and/or the introduction of auto-correlation structures.

Model evaluation was carried out using graphical and analytical methods. In the occurrence model, specificity and sensitivity at the fixed cut-off served as model accuracy indexes. Additionally, the degree of agreement between observed and predicted events was shown on a barplot. In order to test abundance model performance, mean error (E), root mean squared error (RMSE) and modelling efficiency (EF) of the selected conditional model in the logit scale were calculated (Eqs. 7a, 7b and 7c):

$$E = \frac{\sum_{ij} (y_{ij} - \hat{y}_{ij})}{n} \quad (7a)$$

$$\text{RMSE} = \sqrt{\frac{\sum_{ij} (y_{ij} - \hat{y}_{ij})^2}{n - 1}} \quad (7b)$$

$$EF = 1 - \frac{\sum_{ij} (y_{ij} - \hat{y}_{ij})^2}{\sum_{ij} (y_{ij} - \bar{y}_{ij})^2} \quad (7c)$$

Furthermore, occurrence and abundance models were jointly tested on the sample data set. For each year, cumulative observed germination proportion, averaged by measurement period, were compared graphically with that computed from model predictions, previously transformed into the real scale. The Snowdon bias correction was applied to prevent bias derived from back-transformation (Snowdon 1991). Germination occurrence modelling was carried out using PROC NLMIXED in SAS 9.2. All other analyses were assessed in R (R Development Core Team 2009). The nlme package (Pinheiro et al. 2009) was used for the purposes of abundance modelling.

Results

Interannual and seasonal pattern of germination

The earliest germination occurred during the fall following seed deployment for all years included in the study, although the exact date varied from one year to another by up to a month : October 16 (2006–2007), November 7 (2007–2008), November 12 (2008–2009), October 27 (2009–2010) and October 22 (2010–2011). Peak germination periods were in late fall and spring, although a residual germination rate was also observed in winter (2008 and 2011). In contrast, no summer germination was registered during the experiment. The among-year seasonal germination proportions were highly variable (Fig. 2). Autumn germination (from October to late December) ranged from 90 % (2006–2007) down to just 4 % (2008–2009). Spring germination (from late March to May) varied between 20 % (2007–2008) and 4 % (2008–2009). In 2006–2007, no Spring germination was recorded as most seeds had germinated during the fall. The highest within-measurement period proportions of germinated seeds for each year were 8 % (late November 2006), 7.7 % (early November 2007), 7.1 % (November 2008), 11 % (late November 2009) and 7.1 % (late December 2010).

The results from the generalized linear model show that the annual proportion of germinated seeds varied significantly among years (Table 2). In addition, within years variability was relatively high (Fig. 3).

Germination occurrence

Stable convergence was only achieved when understory cover and minimum temperature were excluded from model formulation. Inclusion of year as a random

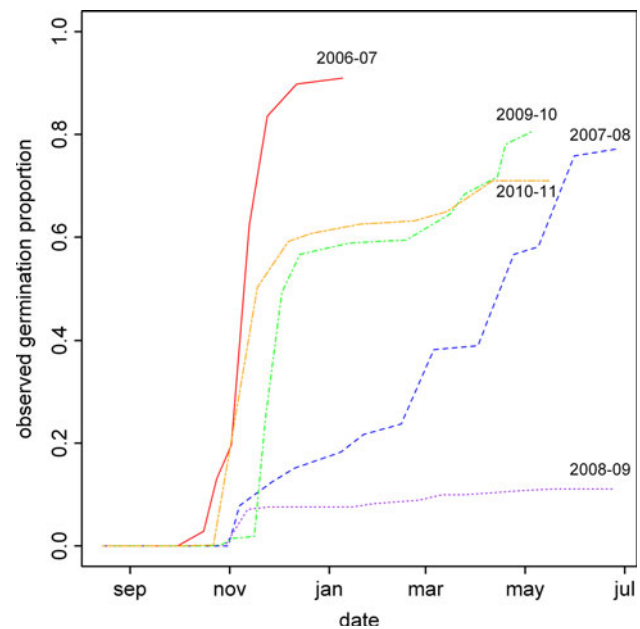


Fig. 2 Observed mean cumulative germination rate over time for the different years of the study. Solid line represents year 2006–2007, dashed line year 2007–2008, dotted line year 2008–2009, dotted/dashed line year 2009–2010, and double-dashed line year 2010–2011

Table 2 Estimates for the binomial model to detect significant differences in germination across years

| | Estimate | SD | z value | p value |
|-------------|----------|--------|---------|---------|
| (Intercept) | 2.3100 | 0.5815 | 3.9724 | <0.0001 |
| 2007–2008 | −1.0925 | 0.7886 | −1.3854 | 0.1659 |
| 2008–2009 | −4.3891 | 0.8529 | −5.1460 | <0.0001 |
| 2009–2010 | −0.8891 | 0.7215 | −1.2324 | 0.2178 |
| 2010–2011 | −1.4204 | 0.6876 | −2.0658 | 0.0388 |

Rejection of null hypothesis ($H_0 = 0$) implies significant differences at least with respect to year 2006–2007, set to zero to avoid overparameterization

component was found to be the optimum variance structure. As regards the formulation of the temperature function, the best fits were achieved when no skewness in germination response was taken into account. Therefore, the parameterization given in Eq. 3 was preferred. The selection of variables was undertaken sequentially. GSF, IPOT and WHC were dropped first as they were found to be non-significant ($p > 0.05$) in all tested circumstances. The model finally included maximum temperature (positive influence) and frost occurrence (negative influence). Details of the selection process are shown in Table 3. The expression for the germination occurrence model was

$$\log\left(\frac{p_{ij}}{1 - p_{ij}}\right) = \alpha_1 + w_l + \beta_1(T_i - \mu_1)^2 + \tau_1 Fr_i \quad (8)$$

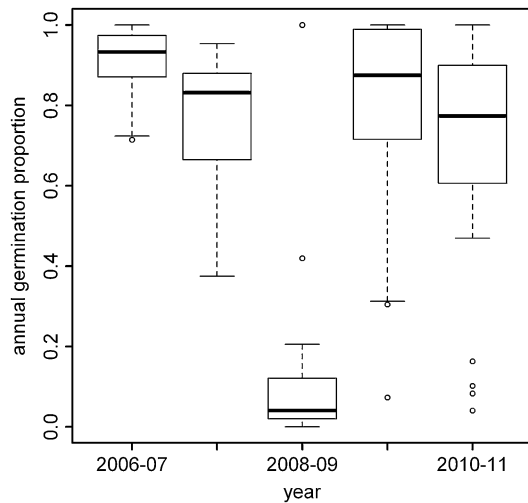


Fig. 3 Distribution of annual germination proportion for each year of study. Within-year variability is achieved by considering seeds points as sample units. Boxes represent interquartile range. Whiskers symbolize percentiles corresponding to 1.5 times the interquartile range

We chose a cut-off of $p_{ij} = 0.5$, as this value exhibits a balanced trade-off between specificity (84.2 %) and sensitivity (84.3 %). The maximum probability of germination

occurrence is expected at a mean maximum temperature of 11.1 °C, whereas negligible values are predicted outside the temperature interval 0–22 °C. For the same temperature, p_{ij} values decrease with the proportion of frost days. Model predictions for the whole range of covariates are displayed in Fig. 4. A comparison between the observed and expected values is shown in Fig. 5. No pattern of discrepancy was found between the data and the model although slightly overestimated predictions are observed each year in the first intervals where germination is detected.

Germination abundance

Logit-transformed (non-zero) pg_{ij} was modelled through a nonlinear mixed model depending on both spatial and temporal variables. The year random effect was found to be the most relevant of all the levels of random variability. The model allowing skewness in response to temperature led to a lack of convergence in the optimization algorithm. Therefore, only the parameterization which does not consider skewness is presented. Parameters linked to frost occurrence, GSF, WHC, and understory type were found to be non-significant regardless of model structure, and hence,

Table 3 Summary of the selection process, parameter p values and fitting statistics for the germination occurrence model

| Skewness | Temp. | μ_1 | α_1 | β_1 | θ | λ_1 | τ_1 | σ_w^2 | AIC | Random effect |
|-----------------|------------|-------------------|---------------|---------------|-----------|-------------|---------------|---------------|----------------|---------------|
| Symmetry | Mean | <0.0001 | 0.0190 | 0.0004 | 0.3055 | 0.0127 | 0.0634 | 0.6674 | 2,072.3 | Year |
| Symmetry | Mean | <0.0001 | 0.1524 | 0.0002 | 0.0253 | – | 0.0299 | 0.8674 | 2,060.2 | Year |
| Symmetry | Mean | <0.0001 | 0.1175 | 0.0003 | 0.1476 | 0.0103 | – | 0.8445 | 2,049.5 | Year |
| Symmetry | Mean | <0.0001 | 0.0363 | 0.0002 | 0.0109 | – | – | 0.2021 | 2,069.1 | Year |
| Symmetry | Mean | <0.0001 | 0.5105 | 0.0004 | – | 0.0012 | 0.0654 | 1.3708 | 2,069.1 | Year |
| Symmetry | Mean | <0.0001 | 0.0795 | 0.0002 | – | – | 0.0118 | 0.1969 | 2,070.4 | Year |
| Symmetry | Mean | <0.0001 | 0.4470 | 0.0003 | – | 0.0036 | – | 0.9551 | 2,050.8 | Year |
| Symmetry | Max | <0.0001 | 0.1205 | 0.0004 | 0.2144 | 0.048 | 0.0056 | 0.8557 | 2,036.5 | Year |
| Symmetry | Max | <0.0001 | 0.1233 | 0.0003 | 0.4953 | – | 0.0030 | 0.8709 | 2,042.6 | Year |
| Symmetry | Max | <0.0001 | 0.7392 | 0.0004 | 0.4874 | 0.011 | – | 0.8787 | 2,065.3 | Year |
| Symmetry | Max | <0.0001 | 0.9187 | 0.0002 | 0.4888 | – | – | 0.9298 | 2,084.1 | Year |
| Symmetry | Max | <0.0001 | 0.2132 | 0.0004 | – | 0.0651 | 0.0061 | 0.7684 | 2,036.7 | Year |
| Symmetry | Max | <0.0001 | 0.5475 | 0.0004 | – | 0.0109 | – | 0.8330 | 2,063.9 | Year |
| Symmetry | Max | <0.0001 | 0.0364 | 0.0003 | – | – | 0.0029 | 0.8209 | 2,041.1 | Year |
| Symmetry | Max | <0.0001 | 0.0025 | <0.0001 | 0.0004 | 0.0087 | <0.0001 | 0.0472 | 2,181.8 | Seed point |
| Symmetry | Mean | 0.0572 | 0.0874 | 0.1511 | 0.2091 | 0.0307 | 2183.5 | 0.0572 | 0.0874 | Plot |
| Skewness | Temp. | α_2 | β_2 | α_3 | β_3 | λ_1 | τ_1 | σ_w^2 | AIC | Random effect |
| Asymmetry | Mean | 0.6363 | 0.0344 | 0.0121 | 0.0083 | 0.0021 | 0.0169 | 0.6836 | 2,108.4 | Year |
| Asymmetry | Mean | <0.0001 | 0.006 | <0.0001 | <0.0001 | <0.0001 | – | 0.04915 | 2,294.4 | Seed point |
| Asymmetry | Mean | 0.401 | 0.2946 | 0.1133 | 0.0982 | 0.0677 | 0.1210 | 0.5503 | 2,265.8 | Plot |

μ_1 represents the temperature value at which germination occurrence is maximized. α_1 , α_2 and α_3 are model intercepts; β_{1-3} , θ , λ_1 and τ_1 are model slopes for temperature, relative humidity, precipitation and frost occurrence, respectively. Parameters linked to the rest of the tested covariates are omitted for simplicity (always non-significant). σ_w^2 stands for variance related to the random effect and Temp. for the thermal variable used (minimum excluded). The complete process is fully detailed when considering year random effect and no skewed response to temperature, whereas only the best model in terms of AIC is shown for all other options. The best model is in bold

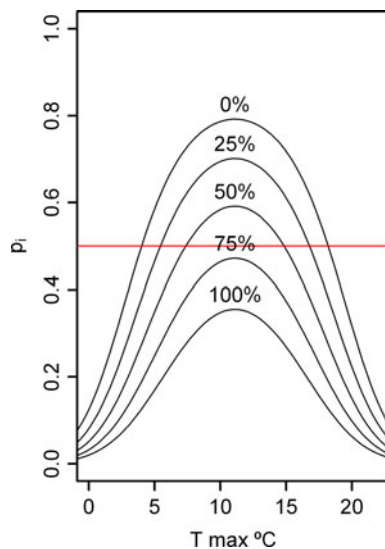


Fig. 4 Plot of predictions for germination occurrence model over mean maximum temperature (T) and varying proportion of freezing days (0, 25, 50, 75, and 100 %). Response variable p_i is the proportion of germinant seed points at interval i . Horizontal line represents the assessed cut-off

they were omitted. Thereafter, variable selection was carried out sequentially although the intercept and parameters related to temperature were retained (Table 4). With regard to the latter, mean temperature proved a better predictor than mean maximum or mean minimum temperature. Furthermore, the preliminary ‘best’ model included relative humidity, mean precipitation and IPOT as explanatory variables having a positive influence on germination abundance.

We found that weighted variance over mean temperature in the form:

$$\text{var}(\varepsilon_{ij}) = \sigma_e^2 \times |T_i|^{2\delta}$$

with δ being an estimated parameter, together with the inclusion of an auto-regressive structure of order 1 (AR-1) produced the best fit and notably diminished AIC values (2,018.018 without correction and 1,908.229 with

correction). Under this new formulation, the IPOT effect was non-significant ($p = 0.4478$) and was therefore excluded from the model (Eq. 9). This model presented an efficiency of 40.04 %.

$$\text{logit}(p_{gij}) = \alpha_4 + w_l + \lambda_2 Pp_i + \frac{1}{\sqrt{2\pi\sigma^2}} \times \exp\left(\frac{-(T_i - \mu_2)^2}{2\sigma^2}\right) \times Hr_i + \varepsilon_{ij} \quad (9)$$

where w_l is the random component of between-year variability affecting α_4 .

The optimum mean temperature for the process is represented by μ_2 estimate (10.37 °C). Back-transformed marginal mean predictions for a wide range of temperature and relative humidity under two rainfall scenarios (Pp_i 0 and 100 %, respectively) are shown in Fig. 6. The closer to the optimum temperature and the higher the relative humidity, the faster the germination rate. Maximum rate when $Pp_i = 100$ % is almost three times as high as when $Pp_i = 0$ %. A negligible germination proportion is expected for mean temperatures below 0 °C or above 20 °C, or for relative humidity levels below 50 %.

The final parameterization for both the occurrence and abundance models is displayed in Table 5.

The combined application of the occurrence and abundance conditional models with the sample data set gave predicted annual proportions of germinated seeds which were highly consistent with those observed (Fig. 7). Predictions for the year 2006–2007 closely match the observed patterns. Estimates for 2007–2008 were slightly biased, with a tendency to overestimate the germination proportion, whereas for the year 2010–2011, the models slightly underestimated germination. In 2009–2010, the slight departure from observations is due to a predicted early germination event in October. This single event altered the whole expected cumulative germination curve, even though the rest of the instantaneous proportions were reasonably precise. Lastly, the models succeeded in properly detecting the unusually low germination occurring in 2008–2009.

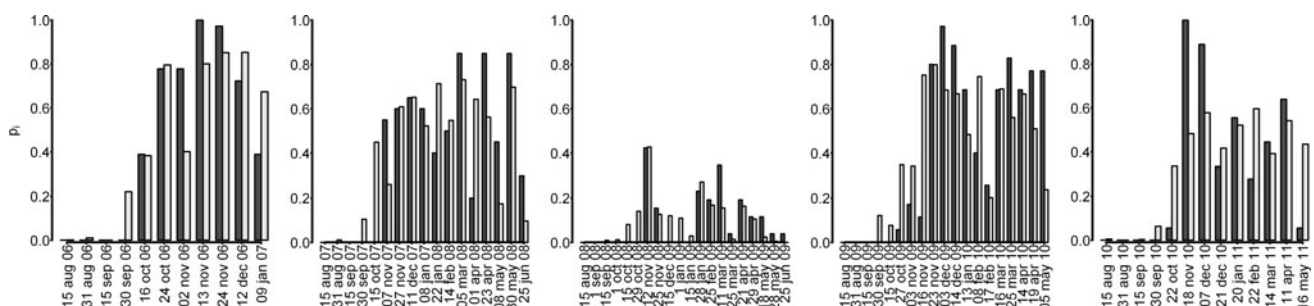


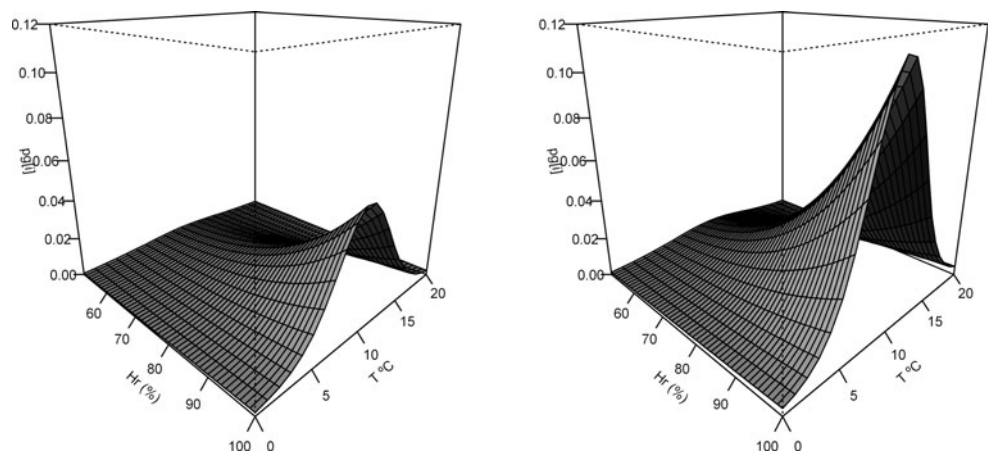
Fig. 5 Observed (black bars) and predicted (grey bars) occurrence proportion (p_i) values for each measurement interval and year

Table 4 Summary of the selection process, parameter p values and fitting statistics for the germination abundance model

| Temp. | μ_2 | σ^2 | α_4 | κ_2 | λ_2 | σ_w^2 | AIC | Random effect |
|-------------|-------------------|-------------------|-------------------|---------------|---------------|---------------|------------------|---------------|
| Mean | <0.0001 | <0.0001 | <0.0001 | 0.0288 | 0.0092 | 0.1893 | 2,018.018 | Year |
| Mean | <0.0001 | <0.0001 | <0.0001 | – | 0.0087 | 0.1816 | 2,020.831 | Year |
| Mean | <0.0001 | <0.0001 | <0.0001 | 0.0271 | – | 0.2178 | 2,022.813 | Year |
| Mean | <0.0001 | <0.0001 | <0.0001 | – | – | 0.2097 | 2,025.722 | Year |
| Max | <0.0001 | <0.0001 | <0.0001 | 0.0411 | <0.0001 | 0.2556 | 2,089.130 | Year |
| Max | <0.0001 | <0.0001 | <0.0001 | – | <0.0001 | 0.2472 | 2,091.392 | Year |
| Max | <0.0001 | <0.0001 | <0.0001 | 0.0343 | – | 0.3087 | 2,102.176 | Year |
| Max | <0.0001 | <0.0001 | <0.0001 | – | – | 0.2996 | 2,104.682 | Year |
| Min | <0.0001 | <0.0001 | <0.0001 | 0.0516 | 0.0007 | 0.1101 | 2,114.380 | Year |
| Min | <0.0001 | <0.0001 | <0.0001 | – | 0.0007 | 0.1040 | 2,116.191 | Year |
| Min | <0.0001 | <0.0001 | <0.0001 | 0.0545 | – | 0.1243 | 2,124.013 | Year |
| Min | <0.0001 | <0.0001 | <0.0001 | – | – | 0.1177 | 2,125.727 | Year |
| Mean | <0.0001 | <0.0001 | <0.0001 | – | <0.0001 | 0.05610 | 2,061.064 | Seed point |
| Mean | <0.0001 | <0.0001 | <0.0001 | 0.1182 | <0.0001 | <0.0001 | 2,070.549 | Plot |

μ_2 represents the temperature value at which germination abundance is maximized. σ^2 is the variance parameter of the temperature normal function. α_4 is the model intercept; κ_2 and λ_2 are model slopes for IPOT and precipitation occurrence, respectively. Parameters linked to the rest of tested covariates are omitted for simplicity (always non-significant). σ_w^2 stands for variance related to the random effect and Temp. for the thermal variable used. The complete process is fully detailed when considering year random effect and no skewed response to temperature, whereas only the best model in terms of AIC is shown for all other options. The best model is in bold

Fig. 6 Marginal predictions assessed through the germination abundance model for a set of varying mean temperatures (T) and relative humidity (Hr) under two scenarios of precipitation occurrence (left no rainfall days, right 100 % of rainfall days within the interval). pg_i is the daily germination rate in real scale



Discussion

Modelling germination

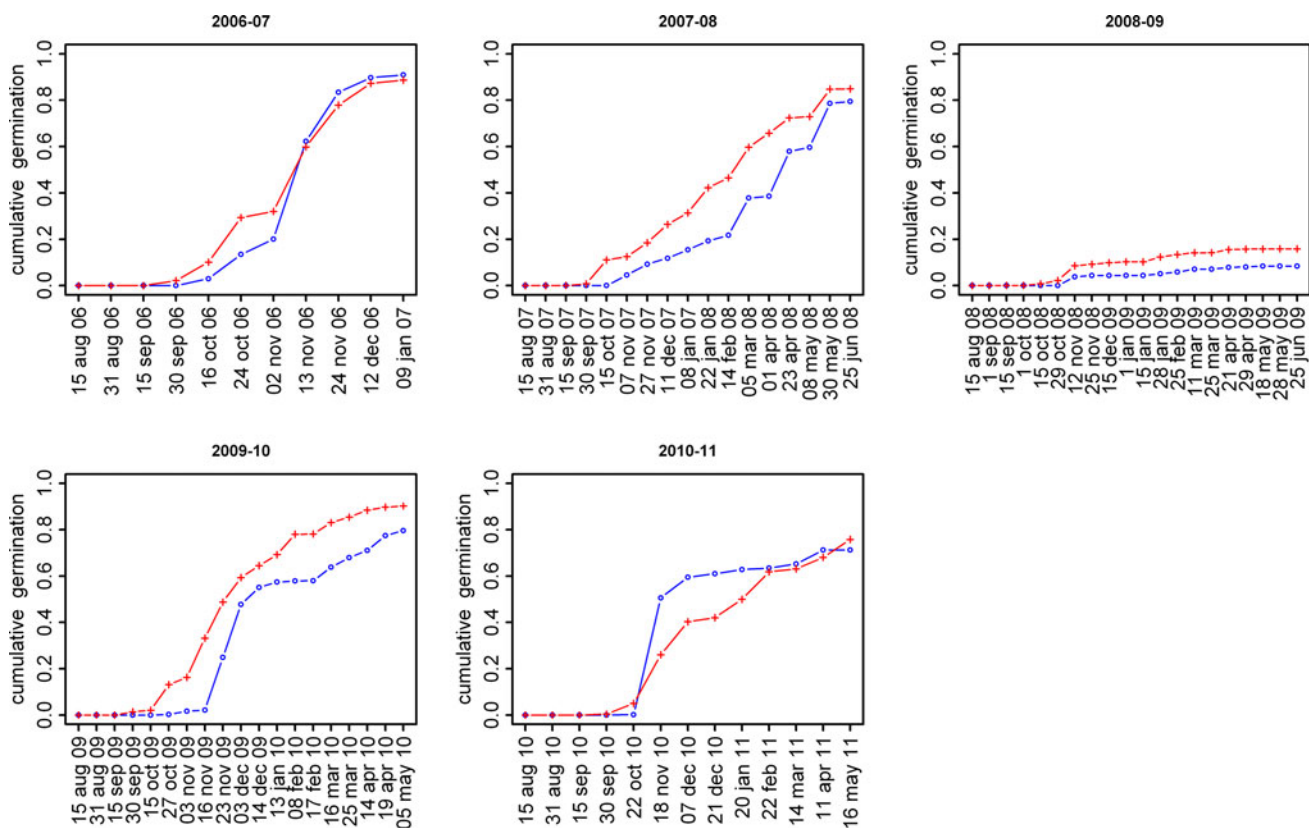
The models presented in this study were based on explanatory variables easily available to forest managers and/or related to silvicultural treatments. Unfortunately, water potential is not among the aforementioned variables, although it is an essential covariate for predicting germination rates. We therefore attempted to include other variables which could, in turn, explain at least part of the variability related to water potential. The variables considered suitable for this purpose were as follows: mean fortnightly relative humidity, proportion of days with precipitation and water-holding capacity.

Temperature is considered to be one of the main factors affecting germination, which requires a suitable thermal interval and will generally occur only within a narrow optimum temperature range (Thornley 1986; Bewley and Black 1994). According to our models, the average mean/maximum/minimum temperature over regular time intervals explains germination response better when skewness is not included in parameterization (range between optimum and base temperature equals that which exists between maximum and base temperature: $T_o - T_b = T_m - T_o$). This is because the explanatory variable summarizes the fluctuating temperatures recorded each fortnight. Despite this fact, temperature itself does produce a skewed response in the species (Magini 1955). The abundance model fitted under the no skewness hypothesis required the use of a

Table 5 Final parameterization, fitting statistics and model evaluation indexes for the selected occurrence and abundance germination models

| Parameter | Value | SD | df | t value | p value | | |
|-------------------------|---------|--------|-----|----------|---------|-----------------|-----------|
| <i>Occurrence model</i> | | | | | | | |
| μ_1 | 11.1042 | 0.4056 | 4 | 27.38 | <0.0001 | AIC | 2,041.1 |
| α_1 | 1.3376 | 0.4323 | 4 | 3.09 | 0.0364 | Specificity (%) | 84.2 |
| β_1 | -0.0266 | 0.0022 | 4 | -12.02 | 0.0003 | Sensitivity (%) | 84.3 |
| τ_1 | -1.9326 | 0.2989 | 4 | -6.47 | 0.0020 | | |
| σ_w^2 | 0.8209 | — | — | — | — | | |
| <i>Abundance model</i> | | | | | | | |
| α_4 | -8.7723 | 0.1962 | 712 | -44.7080 | <0.0001 | AIC | 1,908.229 |
| λ_2 | 0.6818 | 0.1444 | 712 | 4.7217 | <0.0001 | LL | -946.1143 |
| μ_2 | 10.3706 | 0.2288 | 712 | 45.3271 | <0.0001 | E | 0.0247 |
| σ^2 | 52.4262 | 3.2065 | 712 | 16.3498 | <0.0001 | RMSE | 0.9533 |
| δ | -0.1432 | — | — | — | — | EF | 0.4040 |
| φ | 0.4938 | — | — | — | — | AR structure | AR-1 |
| σ_w^2 | 0.1336 | — | — | — | — | Weighed Var | Power |

μ_{1-2} , α_1 , α_4 , β_1 , τ_1 and σ^2 are parameters related to the fixed effects; σ_w^2 is the variance linked to year random effect; δ is the power in the weighed variance; φ is the estimated auto-regressive parameter of order 1. LL is the logarithm of maximum likelihood estimate; E is the mean error; RMSE is the root mean squared error; EF is the efficiency of the model; AR stands for auto-regressive structure and AR-1 is the AR of order 1

**Fig. 7** Observed (circles) and predicted (crosses) cumulative germination rates for each measurement period and year. The latter were achieved from simultaneous conditional predictions of occurrence and abundance germination models

more flexible normal distribution rather than the simpler expression employed in the occurrence model.

In our model formulation, optimum temperature (T_o) is directly estimated as a parameter (μ_1 , μ_2), whereas the

thermal limiting interval is precisely controlled by the occurrence model. The empirical equations developed by Thornley (1986) involve a delaying effect on the initiation of germination that increases asymptotically as temperature

approaches 0 °C. Therefore, an additional thermal covariate representing the proportion of freezing days was included in the model. This was done because the unfavourable effects of very low daily temperatures may not be adequately captured by an average explanatory variable.

The rest of variables considered accounted for light (GSF), overstory (IPOT), and understory (soil cover) conditions. Although GSF and IPOT were measured at seed point level, it is important to note that the range of variation for these variables is a consequence of stand silviculture.

As regards the response variable, the proposed approach directly estimates the instantaneous (fortnightly), non-cumulative germination proportion. If the adequate transformations are undertaken, classic metrics for germination (e.g. time to reach a cumulative germination percentile/germination rate) can be straightforwardly deduced.

The intermittent pattern of germination implied a zero-inflated response variable for germination proportion, which is difficult to model conventionally. Modelling this kind of distribution can be approached through zero-inflated models (Flores et al. 2006; Fortin and DeBlois 2007), even in some cases where data correlation exists (Calama et al. 2011). However, when considering these techniques, classic tools for dealing with further residual assumption violations, such as those present in our data, are not currently implemented in common statistical software. Therefore, in order to avoid an excess of zeros, we modelled germination occurrence and abundance as two separate processes (Woollons 1998).

The selected germination occurrence model only included temporal (thermal) covariates and therefore should be used to generate predictions at stand level. The scarce relevance of random effects other than measurement year suggests that unobserved spatial variability is very low with respect to event occurrence.

Similarly, the germination abundance model only considers temporal fixed effects. IPOT was the only spatial variable for which the associated parameter was found to be significant in some steps of the selection process. However, the auto-regressive structure absorbed the variability explained by IPOT.

The accuracy of simultaneously fitting both models to the sample data set proved to be high. However, the main shortcoming is the tendency to overestimate early germination events. The occurrence model bias appears to be responsible for this, since apparently favourable climatic conditions in the fall did not promote germination events. This particular weakness of the model might be linked to exceptional, unobserved delaying effects, the results of which persist long after their occurrence. From a management point of view, this is not a major concern as long as the model can correctly predict annual germination proportion. However, this issue deserves further research in relation to other ecological applications.

Ecological and management implications

Our findings show that the temporal pattern of germination in *P. pinea* is climate mediated. The *P. pinea* seeds appeared to be extraordinarily sensitive to favourable conditions for germination, even after long periods of adverse conditions, suggesting an absence of dormant pine nuts. Non-dormancy behaviour has been reported for different pine species (Castro et al. 2005; Chambers et al. 1999), although dormancy is not an uncommon mechanism within the genus (Cooke et al. 2002; Krakowski and El-Kassaby 2005; Skordilis and Thanos 1995).

The germination process commences when conditions are within the ecological range described by the occurrence model. These conditions refer exclusively to maximum temperature and frost occurrence, indicating that the readiness to overcome latency is thermally controlled in the species. Accordingly, Thornley (1986) defined delay in germination initiation as a function of temperature. In addition, it can be deduced from model formulation that even within the suitable average thermal range, freezing can condition the initiation of the process. Another reason for delay in germination initiation when carrying out artificial seeding is genetic variability linked to varying origin of reproductive material. This circumstance does not apply in our case, given that seeds come from a restricted area. Once the occurrence conditions arise, germination progression is driven by fortnightly mean temperature, relative humidity and precipitation occurrence. The most favourable mean interval temperature derived from the abundance model is roughly 10 °C, whereas negligible germination is predicted around the upper and lower limits of the interval 0–20 °C. This suggests that temperatures close to the optimum for *P. pinea* (17.5 °C) according to Magini (1955) are more likely to arise at the optimal interval described by our model. In addition, germination increases monotonically with the other two variables as expected, given that they are indirectly related to water potential. This relationship can be illustrated on the one hand by the importance of relative air humidity on water flow towards the top of the profile and the subsequent changes in water potential (Müller 2000). On the other hand, soil water content can be expressed as a function of time since the last significant rainfall (Roman et al. 2000), especially in soils with low WHC, such as those present in the Northern Plateau. Therefore, relative humidity will influence water loss through evapotranspiration whereas precipitation provides water input.

Depending on the species requirements, high stand densities can enhance or reduce germination rates as a result of microclimate modification. Ordóñez et al. (2004) reported increasing germination figures in *Pinus nigra* under closed canopy in typically Mediterranean locations

in the Eastern Iberian Peninsula. Similar results were reported by Lucas-Borja et al. (2011). However, Castro et al. (2005) observed decreasing germination rates in dense stands of *Pinus sylvestris* in mountainous locations of the Iberian Peninsula. In our model selection process, a significantly positive influence of overstory competition (i.e. IPOT) was detected where no auto-regressive structure was applied. Overstory microclimate conditions seem to facilitate the process, which is consistent with the tendency of Mediterranean species. Consequently, lower intensity regeneration felling within the current management range (<50 % of the trees, leaving a density of over 75 stems/ha) will lead to an improvement in germination performance.

Another effect of maintaining higher stand densities would be to decrease the amount of light reaching the soil. Light incidence is generally considered to be positively related to germination. Moreover, it is thought to play an essential role as a gap detection mechanism (Silvertown 1980; Honda and Katoh 2007). However, the parameter reflecting GSF influence on germination was found to be non-significant within the range generated by the two tested stand densities. Similarly, Pardos et al. (2010) concluded that this variable did not influence other physiological processes under current regeneration stand densities. Interestingly, Seiwa et al. (2009) stated that large-seeded, non-pioneer species exhibit little sensitivity to potential germination enhancement signals, probably due to the greater amount of metabolic reserves in larger seeds, which allows a wider range of conditions for germination (Westoby et al. 1992). This supports the findings of this study and the idea of light-independent germination in the species. In this respect, Calama et al. (2012) found that crown influence favours the survival of seedlings and that light stimulation is of little biological importance in *P. pinea* seed germination.

The two spatial effects which are unrelated to plot density in this experimental design were WHC and understory cover. The former was non-significant, probably due to the homogeneity of the soil. The latter was also found to not affect germination, which surely reflects the effect of artificial conditions created when seeding.

In general, the window of optimal climatic germination conditions for *P. pinea* seeds is often narrow. These conditions can occur in the Northern Plateau around November (fall germination) or April (spring germination), although in some years, they may not occur at all. In addition, preliminary assessments of future climate change in Spain (De Castro et al. 2005) point to a decrease in precipitation and increasing mean and maximum temperatures, although minimum temperatures are expected to be more stable, particularly in winter. If these predictions are confirmed, the occurrence of optimal conditions for germination could be seriously threatened. As regards spatial distribution,

very low stand densities such as those resulting from current management methods appear not to enhance the process.

The combination of the common climatic adverse factors occurring in the area and stand structure effect may lead to partial germination failure, which justifies the considerable current seeding effort. However, whereas climatic factors are not controllable, stand density can be easily managed to facilitate seed germination. In this respect, felling intensity is desirable to decrease. Because understocking has been reported to be a source of dispersal limitation in these stands (Manso et al. 2012), denser forests can also reduce the need for direct seeding in this sense. This is particularly true provided that it is possible to predict mast events 1 year in advance (Calama et al. 2011). Furthermore, resulting seedlings would benefit from parent cover in the short term, given the medium shade tolerant behaviour of *P. pinea* (Awada et al. 2003).

Conclusion

The models presented in this study provide promising management tools for describing and predicting *P. pinea* germination occurrence and abundance, particularly as the explanatory variables used are readily available to forest managers. It can be inferred from these models that the temporal factors (climatic variables) are the main determinants of germination success, the suitable germination conditions occurring seldom. However, more progressive felling schedules would encourage germination, partially counteracting adverse climatic events. Denser stands would also rationalize the application of extensive seeding, improving seed dispersal features.

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